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SEASONAL BURROWING BEHAVIOR AND ECOLOGY OF *APORRHAIS OCCIDENTALIS* (GASTROPODA: STROMBACEA)

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The mesogastropod family Aporrhaidae is represented by only three living species comprising the genus *Aporrhais*. *Aporrhais pespelecani* (L.) and *A. serresiana* (Michaud) are restricted to the eastern Atlantic and have been studied by Yonge (1937). [See Fretter and Graham (1962) for a general account of the natural history of these species.] Locomotion in *A. pespelecani* has been examined by Weber (1925) and by Haefelfinger (1968). *Aporrhais occidentalis* (Beck) ranges from Labrador to Massachusetts in the western Atlantic (Johnson, 1930) and is found in depths of water from 10–2000 m (Clarke, 1962). Little information is available on *A. occidentalis*.

Aporrhaids are of particular interest to malacologists because they are the most primitive members of the superfamily Strombacea which includes the widely distributed and conspicuous tropical genera *Strombus* and *Lambis*. According to Cox (1960) and Zittell (1913), aporrhaids first appeared in the Jurassic as the earliest representatives of the Strombacea, and, on the basis of shell structure, Morton (1956) considers *A. occidentalis* to be the most primitive living aporrhaid. As is typical of most members of the Strombacea, the shell of *Aporrhais* is subject to age-dependent changes in morphology. The expanded and thickened outer shell lip of adults is absent in juveniles.

The Aporrhaidae, as well as the related but less ancient Struthiolariidae (Morton, 1951), are known to burrow in soft marine sediments, and Schafer (1972) has commented on the importance of *Aporrhais* in reworking the substrate. Yonge (1937) described the burrowing behavior of *A. pespelecani* and *A. serresiana* under laboratory conditions and concluded that these gastropods are specialized for burrowing in muddy gravel and only rarely move about on the surface of the substrate. Barnes and Bagenal (1952) examined dredged specimens of both species and found that the shells of adult snails were frequently encrusted with barnacles, bryozoans and polychaete tubes. Based on this evidence, they suggested that *Aporrhais* spends more time on the surface of the mud than was previously thought.

The SCUBA techniques used in the present study of *A. occidentalis* have permitted *in situ* tagging experiments and observations on the burrowing of these gastropods in their natural habitat.

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Materials and Methods

During 1973–1976 a population of *A. occidentalis* was studied in 17 m of water at the Isles of Shoals off Portsmouth, New Hampshire (42° 59′ N, 70° 37′ W). The size structure and density of this population was determined through quantitative bottom sampling using SCUBA transects and an epibenthic sled (Hessler and Sanders, 1967).

In April, 1975, individual snails were tagged so that their movements both upon and within the substrate could be followed from month to month. Nylon fishing line was used to affix numbered plastic tags to the shell spires of 20 male and 20 female specimens of *A. occidentalis*. The highly visible tags were buoyant and floated 5–8 cm above the mud at all times. The tagged animals were placed around a cinder-block anchor from which 10 m transect lines were extended in the four compass directions. The transect lines were marked at 1 m intervals so that the snails could be located within the resulting grid system. From May, 1975, to May, 1976, monthly SCUBA dives were made on this site. In addition to daytime observations, night dives were made in summer and winter. Data were taken on the location of tagged snails within the grid system and on whether or not these animals were epifaunal or infaunal.

During each monthly dive, bottom water temperatures were recorded with a hand-held mercury thermometer and notes were taken on the occurrence of potential predators within the transect area. Specimens of *A. occidentalis* were collected each month and preserved for subsequent gut content analyses. Untagged animals were normally used for this purpose, tagged snails being sacrificed only when no others could be found. Empty *A. occidentalis* shells brought up in dredge hauls or found during SCUBA dives were examined for evidence of predation.

In the laboratory, adults and juveniles of *A. occidentalis* were maintained in a flowing seawater system. Burrowing, feeding and copulation were observed and attempts were made to determine the effects of different water temperatures on burrowing behavior.

Results

Specimens of *A. occidentalis* were first observed by the author at the Isles of Shoals during a SCUBA dive in March, 1973. The animals were fully exposed on the level muddy bottom and seemed to be grazing on a thin brown film which covered the substrate. This film was later examined and found to consist of high concentrations of the benthic diatom *Pleurosigma* sp., as well as the decaying remains of several species of macroalgae. Gut content analyses revealed that this material was indeed being ingested along with some sand, sponge spicules and empty foraminifera tests. The shells of these snails were not encrusted with sessile organisms except that the shells of older specimens of *A. occidentalis* were frequently riddled by the boring spionid polychaete *Polydora commensalis* Andrews.

A series of thirty 1 m × 15 m SCUBA transects run at the study site in April, 1974, yielded a total of 28 epifaunal specimens of *A. occidentalis*. Twenty-one of these animals were mature adults with well-developed outer shell lips, while the remaining seven were juveniles ranging in shell length from 20–45 mm. Epi-

benthic sled hauls taken in the same area contained large numbers of juvenile *A. occidentalis* not seen during the SCUBA transects. Ten 0.5 m × 15 m sled hauls yielded 40 young snails and only four adults. Therefore, most of the juveniles in this population were infaunal, while the adults were epifaunal. Laboratory observations over a three year period also showed that juveniles burrow more rapidly and spend more time in the substrate than do adults. Sediment samples taken in April, 1975, contained early post-metamorphic *A. occidentalis* juveniles measuring 1.2–1.5 mm in shell length. Similar sediment samples taken in October, 1975, contained no juveniles smaller than 6.5 mm.

In both 1973 and 1974 the population of *A. occidentalis* at the Isles of Shoals disappeared from the surface of the mud by August and did not reappear until the following February. Although dredging carried out during the winter of 1974–1975 showed that the snails had burrowed at the study site, tagging experiments begun in April, 1975, provided more detailed and quantitative data on seasonal burrowing behavior.

Figure 1 shows the percentages of tagged specimens of *A. occidentalis* found burrowing each month from May, 1975, through April, 1976. Figure 1 also includes monthly bottom water temperatures. Numbers of burrowing animals are expressed as percentages because the total number of snails found each month (both infaunal and epifaunal) varied as a function of water clarity and the time available for searching. Also, the number of tagged snails diminished over time as animals were sacrificed for gut content analyses or were lost due to predation or other factors.

Virtually all of the tagged animals were infaunal from August through October. In November, all of the males remained infaunal but eight of the ten females counted were epifaunal. In December and January the entire population was again infaunal. Most of the tagged *A. occidentalis* were found crawling about on the surface of the substrate from February through June, and 40% were epifaunal in July. Except during the month of November, there were no obvious differences in burrowing behavior between male and female snails.

The results of gut content analyses performed on specimens of *A. occidentalis* collected at the study site suggest seasonal changes in feeding behavior correlated with burrowing. From August through January, all animals had empty stomachs and intestines. Epifaunal snails collected from February through July were actively feeding and had full guts. Furthermore, each of these animals had a well-developed crystalline style in its style sac. Crystalline styles were never found in animals with empty guts.

Gut content analyses were also performed on specimens of *A. occidentalis* collected in deep water by the United States National Marine Fisheries Service and made available by Dr. Roland Wigley of the Woods Hole, Massachusetts, office of the NMFS. Three specimens (two females and one male) dredged from 174 m (42° 05′ N, 69° 50′ W) in November, 1958, had empty guts. Six specimens (three males and three females) collected from 242 m (43° 19′ N, 67° 45′ W) in June, 1961, had full guts.

Because field observations were made only at monthly intervals, it was impossible to obtain detailed data on the mobility of epifaunal snails. From May through July, 1975, when most specimens of *A. occidentalis* were actively feed-

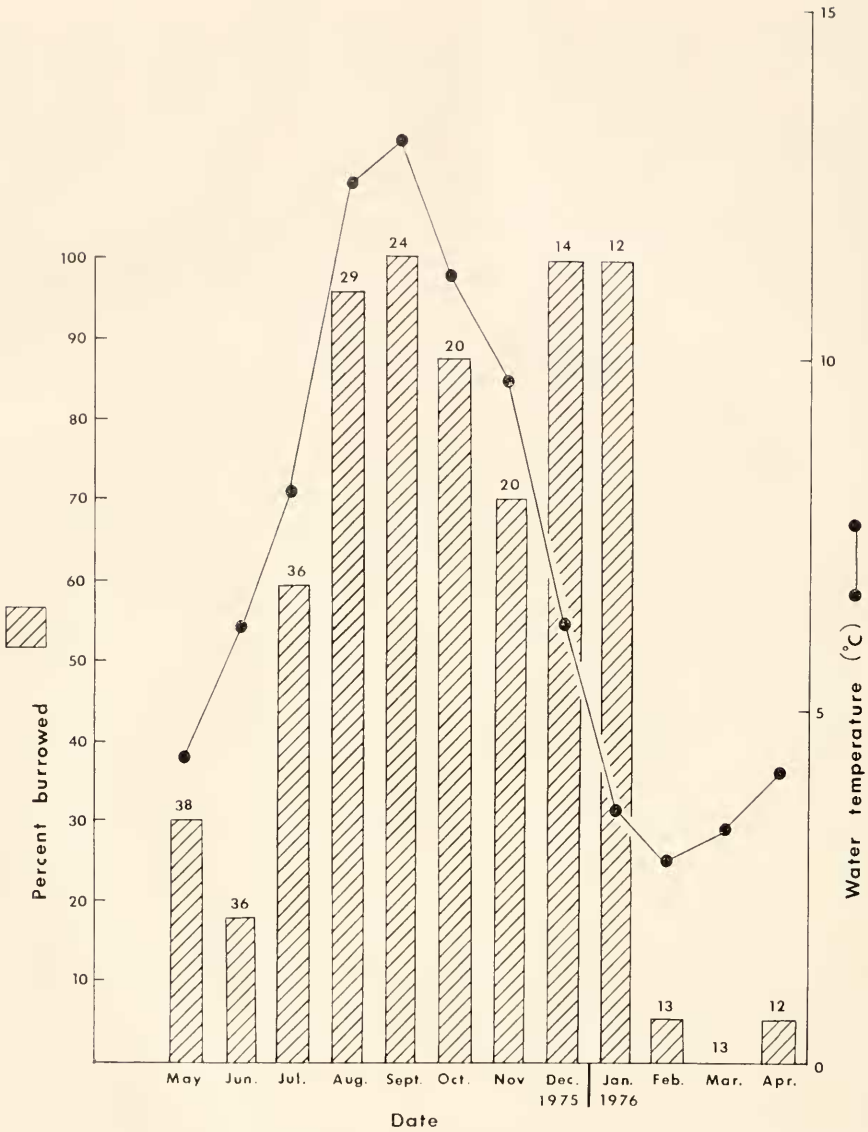

FIGURE 1. Percentages of tagged *A. occidentalis* found burrowing each month at the Isles of Shoals study site. Numbers over histogram bars indicate the total number of tagged snails counted each month. Bottom water temperatures are represented by connected dots. Temperatures represent single measurements taken during monthly dives.

ing on the surface of the substrate, no animal was observed to move more than 10 m from one month to the next. When the population of tagged *A. occidentalis* became infaunal in August, 29 of the original 40 snails were still within the limits of the transect lines. The 11 animals not counted in August may have wandered

away from the study area. However, it is also possible that they were carried off by predators or had lost their numbered tags. From August through January, with the exception of November, no movements of individual snails were noted from month to month. Observations made during night dives showed that although *A. occidentalis* is more active at night than in the daytime during its epifaunal period (February–July), burrowed snails during August–January do not emerge from the substrate at night.

Although copulation was never observed in the field, specimens of *A. occidentalis* kept in the laboratory frequently copulated at night during March and April.

Potential predators on *A. occidentalis* include the carnivorous gastropod *Colus stimpsoni* Morch, the crab *Cancer irroratus* Say, and possibly the molluscivorous wolf fish *Anarhichas lupus* L. *Colus stimpsoni* is present at the Isles of Shoals study site throughout the year and preys on a variety of gastropods. Although *C. stimpsoni* was not observed actually feeding on *A. occidentalis* in the field, instances of predation did take place in the laboratory. *Aporrhais occidentalis* shows a distinct escape response (accelerated locomotion) to the presence of *C. stimpsoni* (Perron, 1978). The crab *C. irroratus* was active at the study site from July through November. Several instances of attempted predation on *A. occidentalis* were observed in the field, and in one case, a crab was seen grasping the numbered tag of a burrowed *A. occidentalis* and pulling the snail from the substrate. In the laboratory, crabs readily devoured juvenile *A. occidentalis* by progressively cracking away the shell aperture until the soft parts were exposed. However, even large specimens of *C. irroratus* (carapace width 6 cm) were rarely able to feed on an adult *A. occidentalis* with well-developed outer shell lips.

In Table I the 71 empty *A. occidentalis* shells collected haphazardly over the course of a year at the Isles of Shoals are classified according to types of visible shell damage. Shells showing crab damage all had apertures which were chipped away in the manner observed in the laboratory and as described and figured by Vermeij (1976). Five of the adult *A. occidentalis* shells showing crab damage had previously been weakened by infestations of the boring polychaete *Polydora commensalis*. Shells so badly crushed that they were reduced to fragments may have been attacked by fish or crabs. Finally, undamaged empty shells may indicate predation by *Colus stimpsoni* or some undetermined cause of mortality.

Laboratory attempts to influence the seasonal burrowing behavior of *A. occi-*

TABLE I

The condition of empty A. occidentalis *shells collected over a one year period at the Isles of Shoals study site. During the same period 143 live animals (60 adults and 83 juveniles) were found.*

Type of shell damage	Number of shells		Probable predator
	Adult	Juvenile	
Chipped outer lip	6	41	Crab
Crushed	2	4	Fish or crab
No damage	11	20	Predatory gastropod

dentalis by manipulating water temperature were unsuccessful. Twenty active epifaunal adult snails collected in March, 1976, were split into two groups and kept at water temperatures of 4–7° C and 13–16° C, respectively. No differences in behavior were noted between the two groups, and all 20 animals remained epifaunal until the experiment was terminated after two months. Specimens of *A. occidentalis* kept in the laboratory for long periods of time tended to become less active and more infaunal. Such animals were also subjected to differing temperature regimes, but no resultant changes in burrowing behavior were observed.

Discussion

The results of the experiments reported here show that the specimens of *A. occidentalis* in the population studied alternate between periods of epifaunal feeding activity and infaunal nonfeeding quiescence. Although tagging data are available only for the year 1975–1976, SCUBA observations during the preceding two years indicate that seasonal burrowing is a regular occurrence in this gastropod. Since *A. occidentalis* has such an extensive bathymetric range, it may not be reasonable to assume that the shallow water Isles of Shoals population is typical of the species as a whole. However, gut content data from specimens collected in deeper water (174–242 m) conform precisely to the pattern observed in the Isles of Shoals population.

The observations of Barnes and Bagenal (1952) on dredged *A. pespelecani* are consistent with a seasonal burrowing pattern similar to that of *A. occidentalis*. The shells of *A. pespelecani* collected by Barnes and Bagenal in April were covered with small newly set barnacles, while "enormously elongated" barnacles were found on specimens dredged in late July. The presence of live barnacles indicates that these *A. pespelecani* were epifaunal during the spring and summer months. Barnes and Bagenal also reported that the shells of dredged juvenile *A. pespelecani* were nearly always free of encrusting organisms. Their suggestion that juveniles spend more time burrowed than do adults is supported by the field and laboratory observations in the present study.

The data in Figure 1 suggest a possible relationship between water temperature and burrowing. At the Isles of Shoals study site, specimens of *A. occidentalis* emerge from the substrate when water temperatures are at their lowest, and remain active until warming takes place during the summer. However, laboratory experiments failed to provide evidence for a causal relationship between temperature and burrowing. Furthermore, since *A. occidentalis* ranges to a depth of 2000 m where seasonal temperature fluctuations are small (Rokop, 1974), temperature would seem an unlikely coordinator of seasonal burrowing. Further research will be necessary to identify the environmental factor or factors which control burrowing in *A. occidentalis*.

Similarly, the available data are not sufficient to explain the role of seasonal burrowing in the life history of this gastropod. It is tempting to suggest that *A. occidentalis* avoids predation by *C. irroratus* by burrowing at the time of year when the crab is most active. Jeffries (1966) has shown that the temperature optimum of *C. irroratus* is approximately 14° C and that these predators become less active and move to deeper water during cold winter months. Nevertheless,

this explanation for the seasonal burrowing of *A. occidentalis* seems questionable when one again considers that the Isles of Shoals population is at the shallow water end of a bathymetric range which extends into the thermally stable depths where predators are presumably not affected by seasonal temperature fluctuations.

Although little is known about reproduction in *A. occidentalis,* Johansson (1948) has studied the reproductive system of *A. pespelecani,* while Lebour (1933) has observed the eggs and larvae of this eastern Atlantic species. *Aporrhais pespelecani* eggs are small (0.25 mm) and are deposited singly or in small groups. The larvae are planktotrophic and undergo considerable growth in the plankton before settling (Lebour, 1933; Thorson, 1946).

The eggs and larvae of *A. occidentalis* have never been reported. However, young benthic animals with shells measuring 1.2–1.5 mm collected by the author in April, 1975, were nearly identical to early post-metamorphic juveniles of *A. pespelecani* figured by Lebour (1933). Since no juveniles smaller than 6.5 mm were taken in October, 1975, it is possible that the breeding season of *A. occidentalis* is similar to that of *A. pespelecani,* with egg laying taking place in early spring (February–March) and larvae settling in April and May (Lebour, 1933). If this is the case, then the reproductive cycle of *A. occidentalis* may consist of a build up of energy reserves during the epifaunal feeding period followed by conversion of this energy into gonad development during the period of infaunal quiescence. The presence of epifaunal nonfeeding females in November is perplexing and may indicate that oviposition takes place at this time rather than in the spring.

Aporrhais is not unique among the Strombacea in possessing burrowing habits. The Struthiolariidae, which probably evolved directly from the Aporrhaidae (Morton, 1951), remain infaunal for long periods while feeding by a ciliary mechanism similar to that of the burrowing, nonstrombacean mesogastropod, *Turritella* (Yonge, 1946). However, there is no suggestion in the literature that burrowing in the Struthiolariidae is seasonal, and unlike *Aporrhais,* these gastropods certainly continue feeding while burrowed. The strombid *Terebellum terebellum* (L.) is also known to be an active burrower (Abbott, 1962), but, again, year round studies have not been carried out.

A seasonal burrowing cycle similar to that of *Aporrhais* has been described for the tropical strombid gastropod *Strombus pugilis* L. by Percharde (1968, 1970). Percharde reports that colonies of *S. pugilis* off the island of Trinidad in the Caribbean burrow in November, cease feeding, and do not resume normal activity until March or April. At the end of this infaunal period the males emerge from the substrate first, while the females remain burrowed for a time and lay their eggs. Percharde (1970) also presents data suggesting similar burrowing behavior in *S. alatus* Gmelin and *S. raninus* Gmelin.

Recent studies by Berg (1974) and Perron (1978) have pointed out the marked homogeneity of locomotory behavior patterns within the Strombacea from the primitive *Aporrhais* to the more highly evolved *Strombus* and *Lambis.* Until year round *in situ* studies have been carried out on additional members of the Strombacea, it will not be possible to determine how pervasive the trend toward seasonal burrowing may be within this superfamily. Nevertheless, the similarities in burrowing habits between *A. occidentalis* and *S. pugilis* probably

reflect the conservative nature of behavioral evolution within the morphologically diverse Strombacea.

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Summary

1. SCUBA observations and *in situ* tagging experiments were carried out on a population of *Aporrhais occidentalis* during 1973–1976. Seasonal changes in burrowing behavior were quantified by determining the percentage of tagged snails found burrowing each month. Gut content analyses were performed at monthly intervals to determine if the intensity of feeding activity fluctuates seasonally. Empty *A. occidentalis* shells were collected and examined for evidence of predation.

2. Specimens of *A. occidentalis* alternate between periods of epifaunal activity and infaunal quiescence. Tagged snails tended to remain burrowed from August through January, but were active on the surface of the substrate from February until late summer. Gut content analyses showed that the snails fed actively during their epifaunal period, but ceased feeding while burrowed.

3. Laboratory attempts to influence burrowing behavior by manipulating water temperature were unsuccessful.

4. Published observations on eastern Atlantic species of *Aporrhais* suggest that seasonal burrowing behavior may be characteristic of the genus.

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